CHAPTER 1. Mangrove Ecology

Key Points

- Mangroves worldwide cover an approximate area of 240 000 square kilometers of sheltered coastlines in the tropics and subtropics.
- Four of the most common ecotypes include fringe, riverine, basin, and scrub forests.
- Mangroves are restricted to the intertidal zone.
- Mangroves in general have a great capacity to recover from major natural disturbances.
- Mangroves maintain water quality by trapping sediments and taking up excess nutrients from the water.

What is a Mangrove?

Ecologically, mangroves are defined as an assemblage of tropical trees and shrubs that inhabit the coastal intertidal zone. A mangrove community is composed of plant species whose special adaptations allow them to survive the variable flooding and salinity stress conditions imposed by the coastal environment. Therefore, mangroves are defined by their ecology rather than their taxonomy. From a total of approximately 20 plant families containing mangrove species worldwide, only two, Pellicieraceae and Avicenniaceae, are comprised exclusively of mangroves. In the family Rhizophoraceae, for example, only four of its sixteen genera live in mangrove ecosystems (Duke 1992).

Where are Mangroves and What do They Look Like?

Mangroves worldwide cover an approximate area of 240 000 km² of sheltered coastlines (Lugo et al. 1990). They are distributed within the tropics and subtropics, reaching their maximum development between 25°N and 25°S (Figure 1.1). Their latitudinal distribution is mainly restricted by temperature since perennial mangrove species generally cannot withstand freezing conditions. As a result, mangroves and grass-dominated marshes in middle and high latitudes fill a similar ecological niche.

The global distribution of mangroves is divided into two hemispheres: the Atlantic East Pacific and the Indo West Pacific. The Atlantic East Pacific has fewer species than the Indo West Pacific (12 compared to 58 species, respectively). Species composition is also very different between the two hemispheres. Out of a total of approximately 70 mangrove species, only one, the mangrove fern, is common to both hemispheres.

Mangrove - a tree or shrub that has evolved the adaptations for growing in the intertidal zone (specifically, adaptations to salinity and flooded conditions).

Figure 1.1 World map showing mangrove distribution

In the continental United States, mangroves are mainly distributed along the Atlantic and Gulf coasts of Florida (Figure 1.2). They also occur in Puerto Rico, the U.S.

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Figure 1.2 Mangrove

Virgin Islands, Hawaii, and the Pacific Trust Territories.
Craighead (1971) estimated a coverage of approximately 1,750 km² of mangroves along the Florida coast, with the highest development along the southwest coast. The Gulf of Mexico and Caribbean regions are characterized by low species richness, with only four dominant species: *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove), *Laguncularia racemosa* (white mangrove), and *Conocarpus erectus* (button-mangrove or buttonwood)

. Black mangroves, however, can be found as far north as Texas, Louisiana, and Mississippi, indicating this species'

greater tolerance to low temperatures and its ability to recover from freeze damage (Markley et al. 1982; Sherrod et al. 1986).



Figure 1.3a Conocarpus (C.E. Proffitt).

Table 1.1 Common mangrove species with common and scientific names and general distribution.

Scientific name	Common name	Distribution
Acrostichum aureum	Mangrove fern	Both hemispheres
Rhizophora mangle	Red mangrove	Caribbean
Avicennia marina*	Grey mangrove	Australia
Avicennia germinans*	Black mangrove	Caribbean, FL, TX, LA, MS, American Pacific Coast
Laguncularia racemosa*	White mangrove	Caribbean, American Pacific Coast
Conocarpus erectus	Button-mangrove or Buttonwood	Caribbean

^{*} shown in Fig. 1.3a, b, c.

The California Current, which limits the northern extent of mangroves along

the Pacific coast of the Americas, brings cold water as far south as Baja California. At the southern tip of this peninsula, mangroves are represented by an occasional, scrubby black or white mangrove. The mangroves of the Pacific Islands are represented by a very different assemblage of species belonging to the Australasian group. Some of the more characteristic genera include *Bruguiera*, *Rhizophora*, *Avicennia*, *Sonneratia*, and *Ceriops* (Tomlinson 1986).



Figure 1.3b Laguncularia Avicennia (C.E. Proffitt).

Mangrove Ecotypes

Mangroves colonize protected areas along the coast such as deltas, estuaries, lagoons, and islands. Topographic and hydrological characteristics within each of these settings define a number of dif-

ferent mangrove ecotypes. Four of the most common ecotypes include fringe, riverine, basin, and scrub forests (Lugo and Snedaker 1974; Twilley 1998). A *fringe forest* borders protected shorelines, canals, and lagoons, and is inundated by daily tides. A *riverine* forest flanks the estuarine reaches of a river channel and is periodically flooded by nutrient-rich fresh and brackish water. Behind the fringe, interior areas of mangroves harbor *basin* forests, characterized by stagnant or slow-flowing water. *Scrub* or dwarf forests grow in areas where hydrology is restricted, resulting in conditions of high evaporation, high salinity, low temperature, or low nutrient status. Such stressful environmental conditions stunt mangrove growth.

Each of these mangrove ecotypes is characterized by different patterns of forest structure, productivity, and biogeochemistry, all of which are controlled by a combination of factors such as hydrology (tides, freshwater discharge, rainfall), soil characteristics, biological interactions, and the effects of storms and other disturbances.

Life History

Mangrove Reproduction and Growth

Most mangroves are hermaphroditic (both sexes are present in an individual organism). Mangroves are pollinated almost exclusively by animals (bees, small insects, moths, bats, and birds), except for *Rhizophora*, which is primarily self-pollinated (Lowenfeld and Klekowski 1992). In most mangroves, germination takes place while the embryo is still attached to the parent tree (a condition called vivipary). The embryo has no dormant stage, but grows out of the seed coat and the fruit before detaching from the plant. Because of this, mangrove propagules are actually seedlings, not seeds (Figure 1.4).

Vivipary as a life history strategy helps mangroves cope with the varying salinities and frequent flooding of their intertidal environments, and increases the likelihood that seedlings will survive. Since most non-viviparous plants disperse their offspring in the dormant seed stage, vivipary presents a potential problem for dispersal. Most species of mangroves solve this problem by producing propagules containing substantial nutrient reserves that can float for an extended period. In this way, the propagule can survive for a relatively long time before establishing itself in a suitable location (McMillan 1971; Tomlinson 1988).

Buoyancy, currents, and tides disperse mangrove propagules and deposit them in the intertidal zone. Once established, the numerous seedlings face not only the stresses of salinity and variable flooding, but also competition for light (Smith 1992). These, in addition to other sources of mortality, cause very low survival rates for seedlings and



Figure 1.3c Avicennia. (C.E. Proffitt).

Hermaphroditic
- Both sexes present in an individual organism.

Vivipary – The condition in which the embryo (the young plant within the seed) germinates while still attached to the parent plant (synonymous with viviparity).

Propagule - Seedling growing out of a fruit; this process begins while the fruit is still attached to the tree. For some species of mangroves, propagules represent the normal, tidally dispersed means of reproduction.



Figure 1.4 Rhizophora trees in Florida, with propagules (C. E. Proffitt).

Evapotranspiration

- The transfer of water from the soil, through a plant, and to the atmosphere through the combined processes of evaporation and transpiration. Evaporation is a function of surface area, temperature, and wind. Transpiration is a process of water loss through leaf stomatal openings, and is related to gas exchange and water transport within a plant. When the stomates open, a large pressure differential in water vapor across the leaf surfaces causes the loss of water from the leaves.

saplings. Determining the age of mangroves is difficult, but flowering individuals have been recorded as young as 1.5 years old. Tree growth,

survival, and the ensuing forest structure are determined by the mangrove forests' ecotype.

There are few estimates of mangrove forest turnover (the time required for the forest to replace itself). Despite a precarious existence in the intertidal zone, Smith (1992) estimates mangrove turnover at 150-170 years. For comparison, estimates for turnover in lowland tropical rainforests is about 118 years (Hartshorn 1978).

Adaptations To Salinity

Mangroves can establish and grow under a relatively wide range of flooding and salinity conditions but are generally restricted to the intertidal zone where there is less competition with freshwater plants. Mangroves have developed a series of physiological and morphological adaptations that have allowed them to successfully colonize these environments.

Mangroves do not require salt water to survive, but because of poor competition with freshwater vegetation and unique adaptations to the intertidal zone, they are generally found under the influence of salt water. Salinity is mainly determined by local hydrology, where input of salt water comes from the periodic tides and fresh water comes from rivers, rainfall, groundwater, and runoff. High evapotranspiration (water loss through the soil and plant leaves) in the tropics and subtropics can increase salinity considerably, especially under environments with restricted water flow. Thus, salinity can fluctuate widely within mangrove forests, both over time and space.

Mangroves have evolved different mechanisms to tolerate high salinities: salt exclusion, salt secretion, and tolerance of high salt concentrations within plant tissues are the main strategies. Most mangroves have developed all three mechanisms, although to varying extents. *Rhizophora*, *Bruguiera*, and *Ceriops* have root ultrafilters that exclude salt while extracting water from soils (Rutzler and Feller 1996). In salt secretion, special organs or glands remove salts from plant tissues. For example, *Avicennia* and *Laguncularia* have special, salt-secreting glands that cause salt crystals to form on the leaf surfaces (Figure 1.5). These crystals then can be blown away or easily washed away by the rain. Leaf fall is another mechanism for eliminating excess salt in mangroves (Kathiresan and Bingham 2001).

Adaptations To Flooding

Mangrove forests are periodically flooded, with the frequency and magnitude of flooding determined by local topography combined with tidal action, river flow, rainfall, surface runoff, groundwater, and evapotranspiration. As with salinity, hydrology in

mangrove ecosystems varies greatly in time and space, and mangrove species differ in their ability to tolerate flooding.

At the intertidal scale, the magnitude and frequency of flooding decreases in a landward direction. Mangrove species often show a distinctive distribution across this gradient, which is the basis for classifying mangroves by lower, middle,

and upper intertidal zones. The lower intertidal zone represents an area inundated by medium-high tides and is flooded more than 45 times a month. The middle intertidal is inundated by normal high tides and it is generally flooded from 20 to 45 times a month. The upper intertidal zone represents areas flooded less than 20 times a month (Robertson and Alongi 1992).

Flooded conditions can decrease soil oxygen, impacting root tissues that need oxygen to metabolize, and toxic substances such as sulfides can accumulate. Mangroves have evolved special morphological adaptations to cope with this lack of oxygen. First, mangroves have shallow root systems to avoid the lack of oxygen in deeper soils. As a result, most of the root biomass is found above 70-cm soil depth (Jimenez 1992). In some species (Avicennia, Laguncularia), roots form an extensive network close to the soil surface. Other species (Rhizophora) form extensive aerial roots (prop roots and drop roots) that help stabilize the tree in unconsolidated sediments (Figure 1.6). Second, aboveground root tissue such as aerial roots (Rhizophora) and pneumatophores (Avicennia, Laguncularia) transport oxygen from the atmosphere to the root system.

These specialized roots contain spongy tissue connected to the exterior of the root via small pores called lenticels. During low tide, when lenticels are exposed to the atmosphere, oxygen is absorbed from the air and transported to and even diffused out of the roots below ground. This diffusion of oxygen maintains an oxygenated microlayer around the roots that enhances nutrient uptake. The microlayer also avoids toxicity of compounds such as hydrogen sulfide that otherwise accumulate under such conditions.

Despite the harsh conditions under which mangrove forests develop, they can form highly diverse and productive communities. Riverine mangrove forests are recognized among the most productive ecosystems in the world, due in large part to low salinities, high nutrient supply, and regular flooding (Day et al. 1987). Less ideal conditions, such as hypersalinity or permanent flooding, severely limit mangrove growth and productivity; extreme conditions, such as restricted hydrology due to impounding, can



Figure 1.5 Close-up of mangrove leaf showing salt crystals (C.E. Proffitt; Gulf of Fonseca, Honduras).

Aerial roots-Roots that are formed in and exposed to air. In mangrove species (e.g., Rhizophora spp.), aerial roots develop into stilt roots (prop roots and drop roots) that anchor into the sediment, offering mechanical support and nutrient absorption.

Pneumatophore - A vertical extension of an underground root, with lenticels and aerenchyma to allow for gas exchange. Pneumatophores are characteristic of trees adapted to flooded conditions (such as Avicennia spp.).

Lenticel – A small, elliptical pore in the periderm that is a means of gaseous exchange.



Figure 1.6 Rhizophora tree (with man in branches) showing prop roots (C.E. Proffitt).

Defoliation - The removal of the foliar tissues of a plant, resulting from mechanical (e.g., hurricanes), biological (herbivore), or chemical agents (e.g., plant hormones).

kill many mangroves. Growth and productivity of mangroves thus ranges widely depending on the conditions under which they grow.

Mangrove Mortality

Mangrove mortality from biological sources includes competition, disease, herbivory predation, and natural tree senescence. All developmental stages are affected, including propagules, seedlings, saplings, and trees. However, mangroves in early stages of development experience higher mortality rates and mortality is generally density-dependent. At the tree stage, smaller trees are at higher risk due to competition with larger trees for light and/or nutrients.

Mangrove diseases include impacts from fungi that defoliate and kill black and red mangroves in Australia and Florida. Insects such as scales and caterpillars cause defoliation and, in Puerto Rico, beetles and other boring insects are known to kill mangroves. *Rhizophora* seedlings are especially vulnerable to mortality caused by the boring beetle. Crabs are important predators of propagules and are a major source of mortality at this stage.

Differences in predation rates on seedlings of different mangrove species may eventually alter species dominance in the adult trees (Smith 1987). Overall, these various biotic disturbances have a relatively minor impact on the mangrove forest when compared with larger-scale environmental impacts.

In contrast with purely biological causes, severe environmental disturbances can inflict larger-scale mortality on mangrove forests. These disturbances include periodic frosts, and hurricanes and other storms, which bring heavy sedimentation (Jiménez and Lugo 1984). In spite of the drastic consequences of massive tree mortality, mangrove forests are generally able to recover.

Habitat Function

Shoreline Stabilization and Protection

Located along the coastline, mangroves play a very important role in soil formation, shoreline protection, and stabilization. The mangrove forest's extensive, aboveground root structures (prop roots, drop roots, and pneumatophores) act as a sieve, reducing current velocities and shear, and enhancing sedimentation and sediment retention (Carlton 1974; Augustinus 1995). The intricate matrix of fine roots within the soil also binds sediments together. Not only do mangroves trap sediments—they also produce sediment through accumulated, mangrove-derived organic matter. Mangrove leaves and roots help maintain soil elevation, which is especially important in areas of low sediment

delivery, such as the southern coast of Florida. By enhancing sedimentation, sediment retention, and soil formation, mangroves stabilize soils, which reduces the risk of erosion, especially under high-energy conditions such as tropical storms.

Coastal protection is also related to the location of mangroves in the intertidal zone. Mangroves are able to absorb and reduce the impacts of the strong winds, tidal waves, and floods that accompany tropical storms, thereby protecting uplands from more severe damage (Tomlinson 1986; Mazda et al. 1997). Even though some of these forces can devastate the mangrove forest, mangroves in general have a great capacity to recover after major disturbances. Mangroves produce abundant propagules, their seedlings grow quickly, and they reach sexual maturity early—characteristics that accelerate their natural ability to regenerate. The speed of recovery, however, depends on the type of forest affected, the nature, persistence, and recurrence of the disturbance, and the availability of propagules.

Detritus – Non-living organic matter that is so decomposed that it is impossible to identify the original parent material.

Animal Habitat and Food Source

Mangroves provide both habitat and a source of food for a diverse animal community that inhabits both the forest interior and the adjacent coastal waters. Some animals depend on the mangrove environment during their entire lives while others utilize mangroves only during specific life stages, usually reproductive and juvenile stages (Yañez-Arancibia et al. 1988).

Mangroves' intricate aerial root system, which is most highly developed within the lower intertidal zone, provides a substrate for colonization by algae, wood borers, and fouling organisms such as barnacles, oysters, mollusks, and sponges. From the diverse group of invertebrates found in mangroves, arthropods, crustaceans, and mollusks are among the most abundant and have a significant role in mangrove ecosystems. As mentioned earlier, some species of crabs, recognized as propagule or seedling predators, can influence mangrove forest structure (Smith 1987), as may seedling predation by beetles or other insects. Crabs and snails, important components of the detritus food chain, help break down leaf litter through grazing.

Shrimp, an important fisheries resource, find food and shelter in mangrove forests. Likewise, commercially important bivalves such as oysters, mussels, and clams are commonly found in and around mangrove roots. Mangroves are also recognized as essential nursery habitat for a diverse community of fish, which find protection and abundant food in these environments, especially during juvenile stages.

Many animals found within mangroves are semi-aquatic or derived from terrestrial environments. Numerous insect species are found in mangrove forests; some play critical roles as mangrove pollinators, herbivores, predators, and as a food source for other animals (Hogarth 1999). Amphibians and reptiles such as frogs, snakes, lizards, and

crocodiles also inhabit mangrove forests. Birds use mangroves for refuge, nesting, and feeding. In Florida and Australia, up to 200 species of birds have been reported around mangrove communities (Ewel et al. 1998). Most of these birds do not depend completely on mangroves, and use these habitats only during part of their seasonal cycles, or during particular stages of the tide. Mammals living in mangrove forests include raccoons, wild pigs, rodents, deer, monkeys, and bats. Finally, turtles, manatees, dolphins, and porpoises can be occasional visitors to mangrove-dominated estuaries.

Water Quality Improvement

Mangrove habitats maintain water quality. By trapping sediments in the mangrove root system, these and other solids are kept from offshore waters, thereby protecting other coastal ecosystems such as oyster beds, seagrasses, and coral reefs from excessive sedimentation. This process can also remove agrochemical and heavy-metal pollutants from the water, since these contaminants adhere to sediment particles.

Mangroves also improve water quality by removing organic and inorganic nutrients from the water column. Through denitrification and soil-nutrient burial, mangroves lower nitrate and phosphorus concentrations in contaminated water, preventing downstream and coastal eutrophication (Ewel et al. 1998). However, the potential of mangroves to "clean" water is limited and depends on the nature of the inputs, and the surface area and nutrient biochemistry of the mangrove forest.

Mangroves have also been used as a tertiary wastewater treatment (Twilley 1998). Even though this practice may increase mangrove productivity by providing nutrients, it should be conducted under carefully designed and monitored conditions. This will reduce negative impacts, such as contamination of adjacent waterways or introduction of invasive species.

Mangrove Economic Value and Uses

There are many mangrove products and services, not all of which are easily quantified in economic terms. Mangrove products can be obtained directly from the forest (wood) or from a derivative, such as crabs, shrimp, and fish. The most common uses of mangrove wood are as a source of fuel, either charcoal or firewood, and as the primary material for the construction of boats, houses, furniture, etc. Given these uses, commercial mangrove production (especially of *Rhizophora spp.*) is common around the world, primarily in Asia (Bandaranayake 1998).

Besides wood, other mangrove products have been exploited commercially. Mangrove bark has traditionally been used as a source of tannins, which are used as a dye and to preserve leather. The pneumatophores of different mangrove species are

used in making corks and fishing floats; some are also used in perfumes and condiments. The ash of *Avicennia* and *Rhizophora mangle* is used as a soap substitute. Other mangrove extracts are used to produce synthetic fibers and cosmetics. Mangroves are also used as a source of food (mangrove-derived honey, vinegar, salt, and cooking oil) and drink (alcohol, wine). For example, the tender leaves, fruits, seeds, and seedlings of *Avicennia marina* and vegetative parts of other species are traded and consumed as vegetables (Bandaranayake 1998).



Figure 1.7 Aerial photo of mangrove forest showing burricane damage in Guanaja, Honduras, taken 14 months after Hurricane Mitch (D.R. Caboon and T.C. Micbot).

Mangroves have great potential for medicinal uses. Materials from different species can treat toothache, sore throat, constipation, fungal infections, bleeding, fever, kidney stone, rheumatism, dysentery, and malaria. Mangroves also contain toxic substances that have been used for their antifungal, antibacterial, and pesticidal properties (Bandaranayake 1998).

Mangrove forests have been widely recognized for their role in maintaining commercial fisheries by providing nursery habitat, refuge from predators, and food to important species of fish and shrimp. Demonstrating a statistical relationship between mangroves and fishery yields has proven difficult, however, because mangroves, seagrasses, and other nearshore habitats are closely linked, and all provide nursery habitat and food for fish (Pauly and Ingles 1999).

Mangrove ecotourism is not yet a widely developed practice, but seems to be gaining popularity as a non-destructive alternative to other coastal economic activities. Mangroves are attractive to tourists mostly because of the fauna that inhabit these forests, especially birds and reptiles such as crocodiles.

Anthropogenic and Naturally Occurring Impacts

Storms and Hurricanes

Mangroves are particularly sensitive to storms and hurricanes because of their exposed location within the intertidal zone, their shallow root systems, and the non-cohesive nature of the forest soils. The effect of storms and hurricanes varies, depending on factors such as wind fields and water levels. Small storms generally kill trees by lightning or wind-induced tree falling, creating forest gaps—an important mechanism for natural forest regeneration. Coastal sedimentation resulting from storms can also lead to mangrove forest expansion.

In contrast, high-energy storms (hurricanes and typhoons) can devastate mangrove forests. Entire mangrove populations can be destroyed, with significant long-term

rise - The worldwide rise in sea level elevation due mostly to the thermal expansion of seawater and the melting of glaciers.

RSLR – relative sea level rise - The net effect of eustatic sea level rise and local geomorphoplogical changes in elevation. Local subsidence can make apparent RSLR much greater than eustatic rise.

Microtidal – A tidal range of less than one meter.

Deposition - The accumulation of material on a substrate. In mangrove systems this term is typically used in relation to accumulation of surface sediment.

effects to the ecosystem (Figure 1.7; Jiménez and Lugo 1985). Mangrove forests that are frequently impacted by hurricanes show uniform tree height, reduced structural development and, sometimes, changes in species composition. However, mangrove forests can recover despite such impacts. How fast a forest recovers depends on the severity of mangrove damage and mortality, mangrove species composition, the degree of sediment disturbance and propagule availability.

Sea Level Rise

In response to global climate change, a gradual increase in sea level rise has been documented since the late Holocene (7000 YBP) and continues to the present. Estimated global rates of sea level rise (eustatic) have been estimated between 1 and 1.8 mm/yr⁻¹ (Gornitz 1995). Local subsidence, uplift, or other geomorphological changes can cause relative sea level rise (RSLR) to be greater or less than eustatic rise. Along the Atlantic Coast of the United States, for example, an estimated RSLR of 2-4 mm/yr⁻¹ has been calculated for a period spanning the last 50 years. In contrast, some areas along the Louisiana coast are experiencing a RSLR of 10 mm/yr⁻¹.

Changes in sea level affect all coastal ecosystems. Changes in hydrology will result as the duration and extent of flooding increases. How well mangrove ecosystems will adapt to this hydrological change will depend on the magnitude of the change and the ability of mangroves to either 1) increase mangrove sediment elevation through vertical accretion, or 2) migrate in a landward direction. The mangrove sediment surface itself is in dynamic equilibrium with sea level, since a local loss of elevation will result in faster sediment accumulation. The problem with accelerated sea level rise is that the rate of rise might be faster than the ability of mangrove forests to accumulate and stabilize sediments. Mangroves can migrate back into previous uplands, but only if there is enough space to accommodate the mangroves at the new intertidal level. Local elevation gradients may make this regression impossible.

Mangroves colonizing macrotidal environments and receiving land-based and/or marine sediments (i.e., riverine mangroves) are generally less vulnerable to changes in sea level rise than are mangroves in microtidal environments, such as in Florida and the Yucatan, or mangroves with restricted hydrology. Land-based and marine sediments increase vertical accretion through direct deposition on mangrove soils. Nutrient and freshwater supply tend to enhance mangrove productivity, which contributes to vertical accretion through the production and deposition of organic matter and root growth. Mangroves under restricted hydrology depend mostly on in-situ organic matter production to attain vertical accretion. Different mangrove ecotypes will therefore have differing sensitivities to increases in RSLR.

Sedimentation

Even though mangroves colonize sedimentary environments, excessive sediment deposits can damage them. Moderate sedimentation is beneficial to mangroves as a source of nutrients and to keep up with predicted increases in eustatic sea level rise. When excessive, sudden sedimentation can reduce growth or even kill mangroves. Complete burial of mangrove root structures (aerial roots, pneumatophores) interrupts gas exchange, killing root tissue and trees. For example, *Avicennia* trees will die after 10 cm of root burial (Ellison 1998). Seedlings are especially sensitive to excessive sedimentation. Under experimental conditions, *Rhizophora apiculata* seedlings had reduced growth and increased mortality after 8 cm of sediment burial (Terrados et al. 1997). Excessive sedimentation can result from natural phenomena such as river floods and hurricanes, but also from human alterations to the ecosystem. Road and dam construction, mining, and dredge spoil have buried and killed mangroves.

Mangrove Pollution

Human-caused pollution in mangrove ecosystems includes thermal pollution (hot-water outflows), heavy metals, agrochemicals, nutrient pollution (including sewage), and oil spills. Oil spill toxicity is discussed in detail in Chapter 2. Thermal pollution is not common in the tropics but, when present, reduces leaf area and causes chlorotic leaves, partial defoliation, and dwarfed seedlings. Seedlings are more sensitive than trees, showing 100% mortality with a water temperature rise between 7 and 9 °C (Hogarth 1999).

Mining and industrial wastes are the main sources for heavy metal pollution (especially mercury, lead, cadmium, zinc, and copper). When heavy metals reach a mangrove environment, most are already bound onto suspended particulates (sediments) and in general do not represent an ecological threat. Although the accumulation of heavy metals in mangrove soils has not been studied in detail, they may decrease growth and respiration rates of mangroves, and will also negatively impact associated animals. Concentrations of mercury, cadmium, and zinc are toxic to invertebrate and fish larvae, and heavy metals cause physiological stress and affect crab reproduction.

Runoff from agricultural fields represents the main source of organic chemical contamination in mangrove ecosystems. Little is known about the effects of pesticides in mangroves and associated fauna, although chronic effects are likely. As with heavy metals, many of these compounds are absorbed onto sediment particles and degrade very slowly under anoxic conditions. Despite the possibility of burial, heavy metals and pesticides may bioaccumulate in animals that use mangroves (especially those closely associated with mangrove sediments), such as fish, shrimp, and mollusks.

Nutrient pollution in mangroves can have various effects. Sewage disposal under carefully managed conditions can enhance tree growth and productivity as a result of

Chlorosis/chlorotic

 abnormal condition characterized by the absence of green pigments in plants, causing yellowing of normally green leaves.

Anoxic - Without free oxygen. Aerobic metabolism (e.g., bacterial respiration) can consume dissolved free oxygen in water and soils, resulting in anoxic conditions that are detrimental to oxygenbreathing organisms. (p.19)

Bioaccumulate

- Uptake of dissolved chemicals from water and uptake from ingested food and sediment residues. (p. 19)

Anchialine ponds - A rare Hawaiian ecosystem, consisting of pools with no surface connection to the ocean, but affected by tides. These pools have a characteristic water quality and support an assemblage of animals and plants, many of which are endangered.

added nutrients, especially nitrogen and phosphorus (Twilley 1998). However, if the rate of disposal is greater than the uptake rate (a function of forest size and mangrove ecotype), excessively high nutrient concentrations will result. This causes excessive algal growth, which can obstruct mangrove pneumatophores and reduce oxygen exchange. Algal mats can also hinder growth of mangrove seedlings (Hogarth 1999). Excessive microbial activity accompanies high levels of nutrients, and depletes oxygen in the water, which is harmful for mangrove-associated aquatic fauna.

Development and Forest Clearing

Despite the ecological and economic importance of mangroves, deforestation has been widespread. Deforestation has mostly been related to firewood and timber harvesting, land reclamation for human establishment, agriculture, pasture, salt production, and mariculture. Tropical countries have sustainably harvested mangrove wood for generations, but increasing populations have led to unsustainable practices. Human activities have had varying degrees of impact: a residential project in Florida destroyed approximately 24% of mangrove cover (Twilley 1998). In Ecuador, the leading exporter of farm-raised shrimp, approximately 45-63% of mangrove habitat in the El Oro River has been lost due to mariculture pond construction (Twilley 1989).

Despite laws established for mangrove protection in many different countries, unregulated exploitation and deforestation continues. In the Philippines, approximately 60% of the original mangrove area has disappeared. In Thailand, 55% of the mangrove cover has been lost over about 25 years. Eventually, the overexploitation of mangrove forests will degrade and, ultimately, lose habitat, increase shoreline erosion, damage fisheries, and lose services derived from these ecosystems.

Invasive Species

Mangroves have been successfully introduced in several tropical islands where they did not occur naturally, and may thus be considered an invasive species. Hawaii is an example of such a case, where the proliferation of *Rhizophora mangle* has deteriorated habitat for some endemic waterbirds and has damaged sensitive archaeological sites. The proliferation of mangroves has also been linked to the premature infilling of a unique Hawaiian aquatic ecosystem called anchialine ponds. Despite providing useful environmental services (e.g., shoreline protection, organic matter production, and water quality), the mangroves may proliferate in these foreign environments and seriously impact the native flora and fauna. The cost of their removal has been reported to vary from \$108,000 to \$377,000 per hectare (Allen 1998).

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